

ARTHROPLEURIDA

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[Hunterian Museum, University of Glasgow] [The writer is indebted to Dr. S. M. MANTON, F.R.S., for helpful discussion of *Arthropleura* and living myriapods, and to Dr. J. K. INGHAM for much assistance in reconstructing *Arthropleura*]
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INTRODUCTION

The arthropleurids are an extinct group of rare gigantic centipede-like arthropods which inhabited coal swamps during Late Carboniferous times. The group, as here interpreted, is known with certainty to contain only the eponymous genus *Arthropleura*, although two other genera may be related, one of them even ancestral.

There has been much discussion of the affinities of *Arthropleura*: it has been referred to Chelicerata, Trilobitomorpha, Crustacea, Myriapoda, and Arthropoda *incertae sedis*. The Arthropleurida is here tentatively regarded as a unique class of myriapods, showing parallel evolutionary trends to the polydesmid diplopods, but differing from them in the number of segments in and structure of the limb, and in the gigantic length attained. Although arthropleurids are rare, their huge size makes them suitable for detailed study and the limb is as well known as that of any fossil arthropod. In terms of body size, *Arthropleura* can claim to be the largest terrestrial arthropod known.

MORPHOLOGY

The most striking feature of *Arthropleura* is its colossal size. The largest most complete specimen known (7) is two feet

eight inches long (80 cm.), yet isolated segments and paratergal folds which have been found indicate that animals up to six feet (180 cm.) in length must have existed (9). Small individuals representing young instars are also known, however, and the most complete of these (described as the separate species *A. moyseyi* by CALMAN but subsequently regarded as a juvenile *A. armata*) is 65 mm. long (Fig. 386).

The cuticle seems to have been relatively thin for such a large arthropod: WATERLOT states that its maximum thickness is 2 mm. Over the large rosette plate (shown on Figure 391,C) the space between internal and external molds measures less than 0.12 mm., indicating a cuticle of this thickness. In flattened, carbonized limbs, details of the morphology of one surface are commonly impressed through onto the other (see Fig. 389,C), as may also be details of the venation of underlying plant fragments. There is no indication that the cuticle was mineralized during life and it was probably only toughened by sclerotization.

The juvenile *Arthropleura armata* referred to above (Fig. 386) has the course of the intestine indicated in the hind two-thirds of the body by a zone of darker iron-stone packed with plant fragments. It occupies just more than half the width of the axis and is confined to it, although secondarily pressed through the tergites.



FIG. 386. Rubber cast from external mold of almost complete juvenile *Arthropleura armata* JORDAN & MEYER (holotype of *A. moyseyi* CALMAN), head slightly displaced, dorsal, U.Carb., Eng., $\times 2$ (Rolfe, n).

HEAD

The head is known from only one specimen (Fig. 386). It is poorly preserved, but can be seen to be broader than long and approximately one-third the greatest width of the body. The specimen shows the ventral surface of the head, with an anteriorly fimbriated, curved appendage forming the side of the head and thus resembling the myriapod mandible in position.

BODY

The body is elongate and of almost uniform width but tapers anteriorly and posteriorly (Fig. 387). It is longitudinally trilobed dorsally, forming a median axis with lateral paratergal folds. The tergites are dorsoventrally depressed and there is no reason to believe that they were much more convex in life.

The number of body somites is unknown; the two almost complete specimens described have 27 and 23 postcephalic somites preserved, but both specimens are somewhat disarticulated and these numbers are minimal. No telson has yet been observed.

Tergites of the somites vary in shape, size, and ornament according to their position on the body and according to the age of the individual. Anterior tergites are narrower, show more anteriorly oriented paratergal folds and bear fewer tubercles and spines than those in the central region of the body (Fig. 388); the first three tergites are also shorter than succeeding ones. Posteriorly the tergites gradually diminish in breadth and have the paratergal folds increasingly directed rearward. Each tergite overlaps the next somite behind by approximately one quarter of its length. This region of the tergite is only finely tuberculate and bears a transverse rib and furrow marking it off from the main area of the tergite.

The axial region of each tergite is rectangular and separated from the two lateral triangular paratergal folds by furrows. From this furrow and the frequent occurrence of paratergal folds isolated from axes most authors have deduced that the paratergal folds were movably articulated with the axis, and indeed the name *Arthropleura* refers to this feature. It is possible, however, that the split sometimes seen separating paratergal folds from the axis is due to flattening of the originally more convex segment and not to any original hinge structure.

Both axis and paratergal folds commonly bear all sizes of tubercles, grading from large, posteriorly directed, blunt conical spines to fine granules. Each paratergal fold also bears two recurved keels, the crests of which are serrate-tuberculate distally. The tuberculation pattern and direction of the prominent, main paratergal keel have been

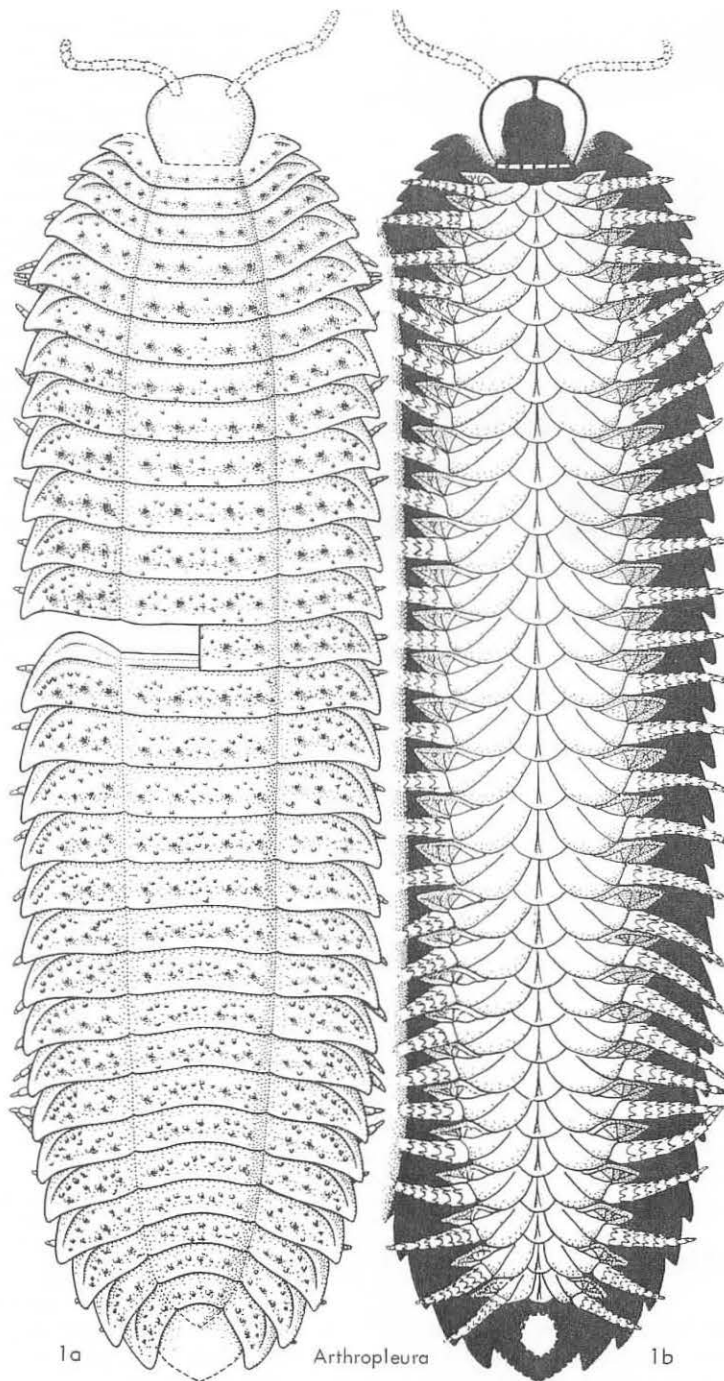


FIG. 387. Reconstruction of *Arthropleura armata* JORDAN & MEYER, dorsal, ventral. Half of one tergite removed to show anterior border of underlying tergite; no limbs shown on first trunk somite. Interrupted lines indicate restored regions of body, approx. $\times 0.1$ (16).

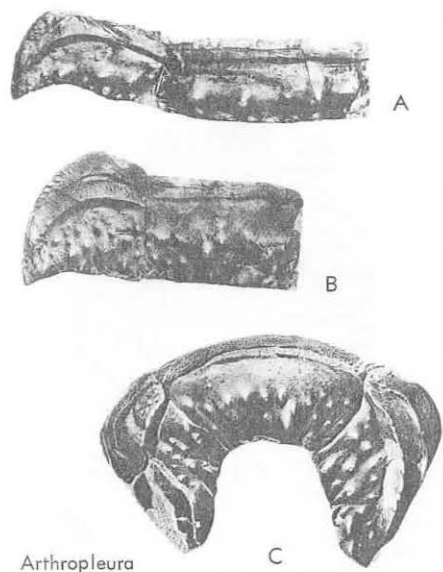


FIG. 388. Isolated tergites of *Arthropleura armata* JORDAN & MEYER, dorsal, Carb., Saar, $\times 0.5$.—A. Axis and left paratergal fold from anterior body somite showing anteriorly directed paratergal fold and sparse tuberculation (19).—B. Axis and left paratergal fold from middle body somite (19).—C. Complete last body somite (pretelson) (1).

the two chief characters used in differentiating species of *Arthropleura*, although no statistical study of these highly variable characters is yet available.

The sternite is only seen preserved as a triangular area between the bases of the ventral limbs. It bears a shallow median longitudinal sulcus and has a convex posterior margin. According to WATERLOT (19), the integument is either smooth or finely granulose. The pleuron immediately underneath the paratergal folds is finely pitted (or granulose?) and wrinkled, but otherwise featureless. Other structures which probably comprise the pleuron are dealt with in the following section.

LIMBS AND ASSOCIATED STRUCTURES

Each segment bears one pair of limbs ventrally inserted almost halfway between the mid-ventral line and tips of the paratergal folds. Prior to 1934 all authorities agreed that the limb of *Arthropleura* was uniramous. After a most exhaustive study

of the available material WATERLOT (19) concluded that the limb was biramous, comparable to that of the trilobite in basic structure yet even more primitive in that the two rami were identical in form. This interpretation was challenged by STØRMER (1944), and subsequent study by ROLFE and INGHAM (16) of largely uncrushed material (Fig. 389) vindicated STØRMER's view that the limb is uniramous. A reconstruction of the limb is shown in Figure 390.

It is not yet known whether the limb comprises eight, nine or ten segments. The clawlike pretarsus numbered 10 may not be an independent segment and the posterior, incompletely preserved segment 1 may not be a limb segment but a subcoxal sclerite. Thus either it, or segment 2, represents the coxa. Each segment bears distally a pair of stout outwardly and downwardly directed spines. Segment 8 is consistently longer than other segments, although one specimen (Fig. 389,B) is known in which a more proximal segment is longest, suggesting either that this limb is abnormal owing to regeneration after an injury, or that the segment number is not constant for all limbs. The anterior surface of the limb is smooth, whereas the posterior face bears tubercles, some of which show a terminal pore suggesting the original presence of a seta. Both surfaces of the limb show sharp linear invaginations of the cuticle, which on the proximal regions of the limb run obliquely across the segments. These form ridges on the inside of the limb, probably analogous to the *costae coxales* of Recent centipedes, and doubtless served both to strengthen the leg joints and to provide sites for the attachment of limb muscles. It was these ridges, and especially that on the proximal region of the posterior face of the limb, that WATERLOT misinterpreted as the dorsal edge of one ramus of a biramous limb overlapping the other ramus. On the posterior face of the limb, the invaginations of segments 1, 2, and 3 have a radial disposition (Fig. 390) and when found isolated these segments may be mistaken for a rosette plate and its associated anterior face of segment 2.

The more proximal structures associated with the limb may be referred to as the rosette plate, B plate and K plate. The two

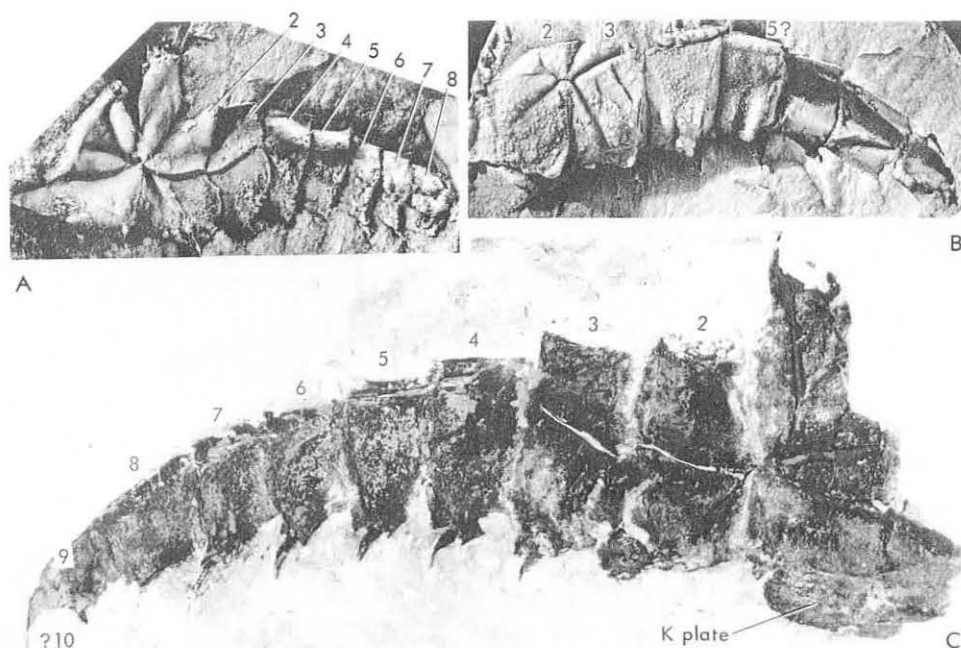


FIG. 389. Limbs of *Arthropleura*.—A. Rubber cast from external mold of anterior face of left leg of young individual showing B and rosette plates and segments 2-8, Carb., Eng., $\times 2.3$.—B. Right leg, showing internal mold of posterior face of segments 2-5? and external mold of anterior and dorsal surface of distal segments (one segment lacking in this individual, possibly due to regeneration), Carb., Eng., $\times 2.3$.—C. Complete flattened right leg, anterior view, but with features of posterior face of limb impressed through. Shows K, B, and rosette plates and segments 2-10, Carb., Neth., $\times 1.1$ (16).

latter terms were introduced by KLIVER (1884) and ANDRÉE (1) to signify the basal segment and supposed gill lamella (*Kiemenblätter*) of the limb. All three structures are here interpreted as sclerotized regions of the body wall (*i.e.*, pleurites or subcoxal sclerites), as in living centipedes (MANTON 1965; SNODGRASS 1952), rather than true limb segments, although there must still be debate on this point as outlined below. Since the function of the rosette plate is only a passive one, therefore, it is suggested that the hitherto used term "rosette organ" be abandoned.

The rosette plate is an elongate, convex plate, bounded anteriorly and posteriorly by convex borders, and divided into a number of lobes by deep subradial sulci. WATERLOT (19) devised the notation given in Figure 390 for these lobes. Most of the lobes shown usually are present but in older individuals the number of adventitious lobes is greater and the lobes tend to be more irregular in

form (Fig. 391). Several of the lobes bear mammiform tubercles with central pores which were originally setiferous. Young individuals lack this tuberculation, however (Fig. 389, A).

The B plate is a triangular convex posterior extension of the rosette plate, from which it is separated by a deep sulcus oriented almost perpendicular to the sagittal plane of the body (Fig. 392). Such a huge terrestrial creature as *Arthropleura* would need massive buttressing of the limb bases at their insertion on the body wall to enable limb movement to take place. It seems likely that the rosette and B plates provided such reinforcement of the pleuron, and their situation in front of the limb suggests that the limbs thrust backward and downward in normal locomotion.

In an attempted analogy with *Limulus*, WATERLOT (19, 21) regarded the C lobe of the rosette plate (Fig. 390) as a precoxal segment, which attached the limb to the

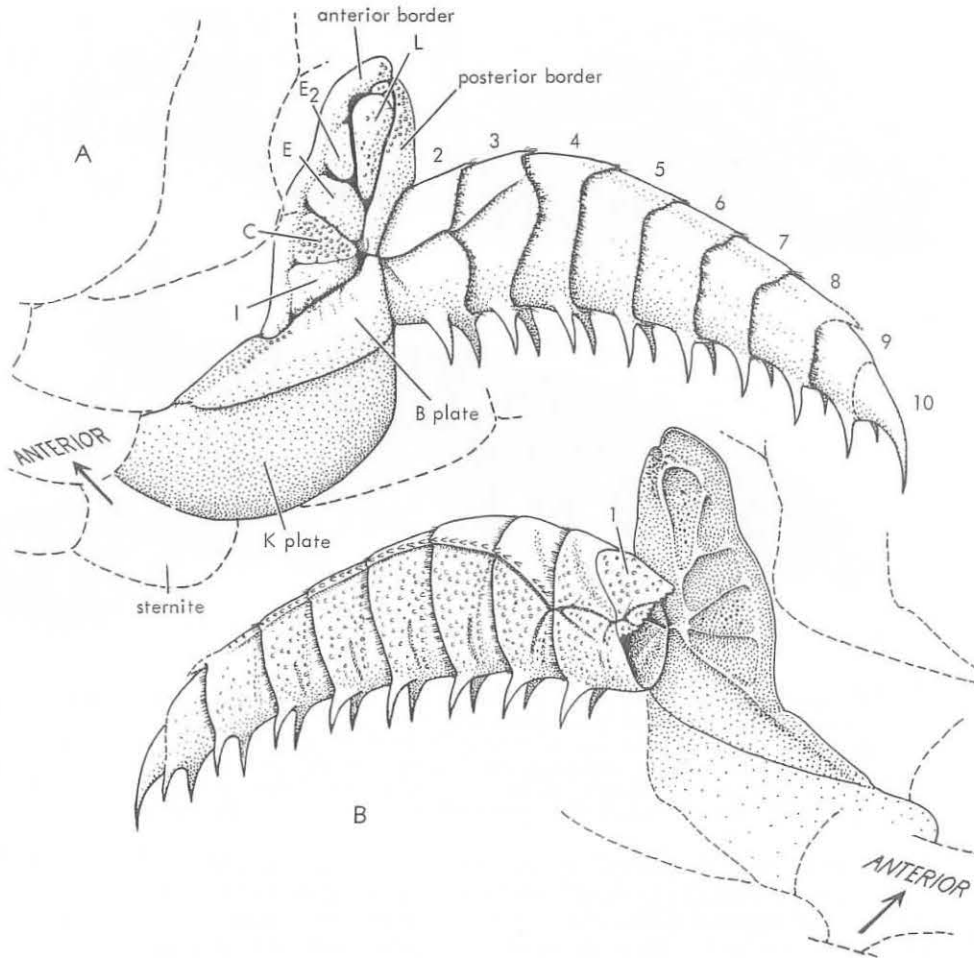


FIG. 390. Reconstruction of left leg of medium-sized adult *Arthropleura*. Both views are taken obliquely to emphasize the morphology and the limb is thus slightly foreshortened. Interrupted lines indicate most of sternite, *K*, *B*, and rosette plates of body somite immediately in front and posterior edge of *B* plate of somite immediately behind, and serve to orient the limb relative to the body wall. The letters show WATERLOT's notation for lobes of the rosette plate—*A*. Anteroventral view.—*B*. Posterodorsal view $\times 1$ (16).

body wall and articulated with it by the insertion of the *C* lobe between the *I* and *E* lobes (supposedly evaginations of the sternum). As RICHARDSON (14) has pointed out, however, WATERLOT's schematic cross section of a limb-bearing somite (19, fig. 27; 21, fig. 4) is misleading in showing a leg suspended wholly outside the body, with no provision for the passage of leg muscles into the body. Furthermore, to separate off the *C* lobe as a distinct limb segment is clearly unjustifiable. It is difficult to accept

WATERLOT's interpretation of the homologies of the other basal limb structures which followed from his view. For example, it would be impossible to recognize as such a precoxa which articulated with the basis and yet not with the coxa, as WATERLOT's latest reconstruction (21) implies.

The frequent occurrence of isolated well-preserved rosette plates with their *B* plates attached implies that the surrounding pleuron consisted of unsclerotized integument, as must also the intersegmental mem-

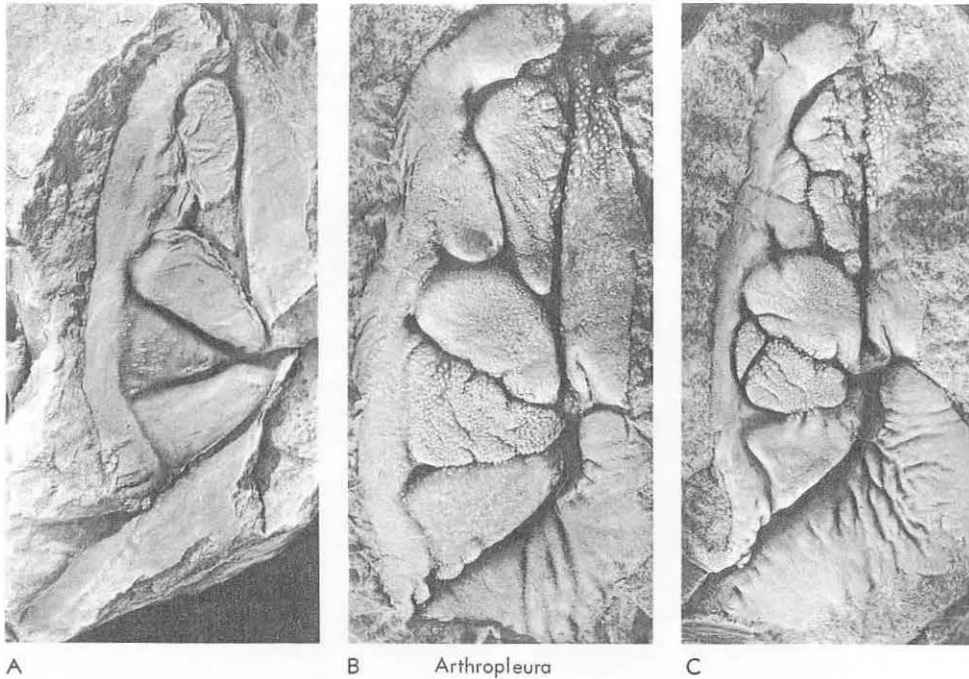


FIG. 391. Left rosette plates with portion of *B* plate attached of *Arthropleura* to show increase in tuberculation and number of adventitious lobes with size (i.e., age).—A. Westphal., Neth., $\times 1.8$.—B. Penn., USA (Ill.), $\times 1.5$.—C. Penn., USA (Ill.), $\times 1$ (Rolfé, n).

brane between these plates and limb segment 2.

The *K* plate ("ventral lobe" of STØRMER, 1944; "epipodite" or "gill plate" of other authors) is a thin plate, usually oval and irregularly wrinkled. In isolated limbs and limb fragments this plate appears pitted and commonly occurs with its anterior edge tucked under the incurved posterior edge of the *B* plate, but it may also overlap the same plate and WATERLOT has suggested that it is only attached by a small tongue to the "distal" end of the *B* plate; the variable position of the plate suggests that it is only attached by unsclerotized integument. The original position of the plate is therefore doubtful. If the pitting is regarded as the internal expression of tuberculation, then this plate would seem to be part of the posterior face of the limb, only secondarily shifted into an anterior position. The consistent position of the overlapping *K* plates preserved *in situ* on the flattened specimen shown in Figure 392 argues against this,

however. Differences in appearance between *K* plates on isolated limbs and those *in situ* probably reflect their different attitudes during flattening. The *K* plate has only one surface and it is therefore difficult to interpret it as a lamellar gill, as originally suggested by KLIVER and accepted by subsequent authors. If the *K* plate could be shown to be a gill plate it would imply that the *B* and rosette plates were coxal structures. ANDRÉE (1) and PRUVOST (1919) thought that the *K* plates might represent oostegites. The *K* plate is here interpreted as a convex, less sclerotized area of the ventral integument. The function of the plate, if it is not just an intercalated sclerite, must remain doubtful until its structure and position on (or even within) the body are better known. It is tempting to regard it as homologous with either the coxal sac or eversible vesicle of modern myriapods; VERHOEFF suggested that the supposed coxal sacs of the Myriapoda Archipolypoda enabled their owner to respire on land and

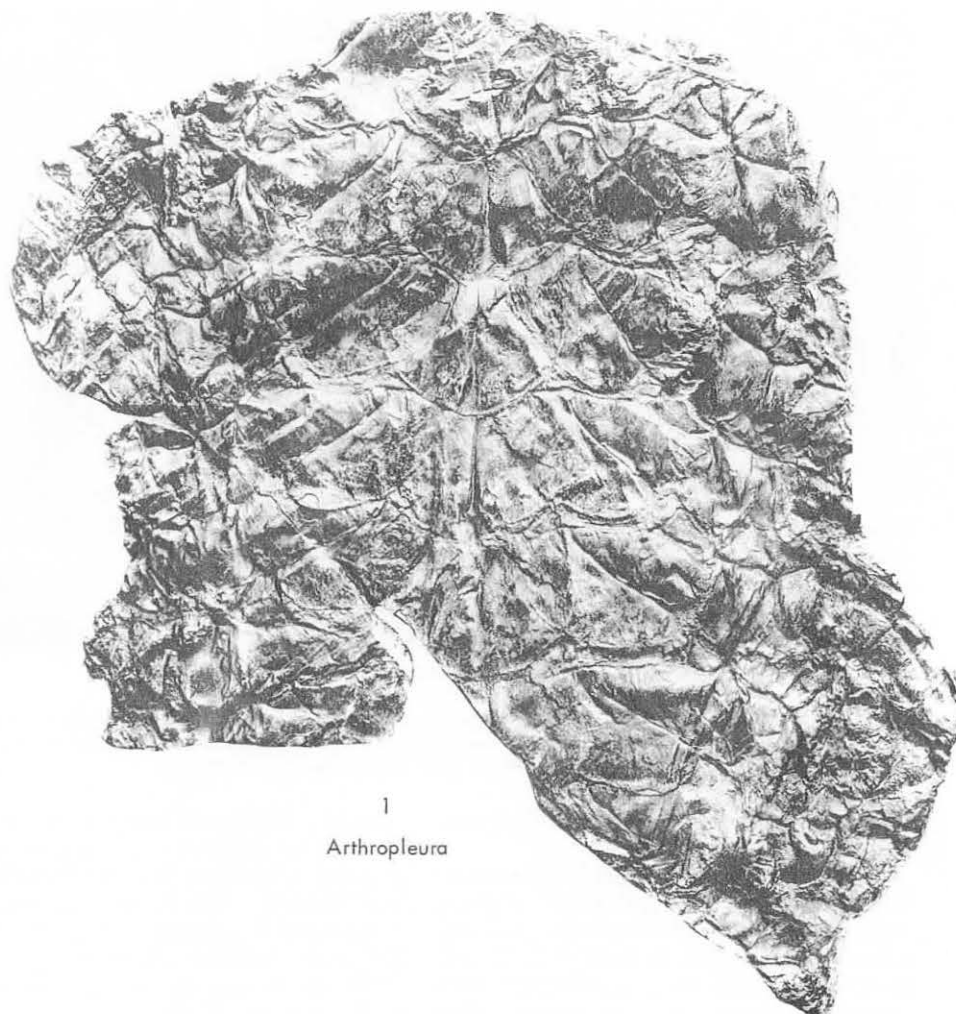


FIG. 392. Pedigerous ventral surface of small specimen of *Arthropleura armata* JORDAN & MEYER. This specimen, which is only half of an originally larger specimen, shows 7 pairs of limbs flattened *in situ* onto 6 sternites. Most of the rosette plates are concealed beneath limbs of the somite immediately in front, but one can be seen at the top right, Carb., Saar, $\times 1$ (19).

could be everted to function as gills when in water.

In 1947 WATERLOT (20) described two limb segments which he suggested belonged to a gnathobasic cephalic limb. Additional evidence is required before this view can be confirmed or denied.

PALEOECOLOGY

Most specimens of *Arthropleura* have been found either in nonmarine shales or

clay ironstone concretions of the Coal Measures. The few which have been found in undoubted marine strata were probably washed in from nonmarine sources. Finds are characteristically associated with plants, the delicate fronds of which are so well preserved that WATERLOT (19) inferred that they could not have drifted far. This association with abundant plants, commonly in roofs of coal seams, suggests that both *Arthropleura* and vegetation were drowned by the submergence of the forest swamp at

the initiation of another cyclothem. Furthermore, the most abundant finds of *Arthropleura* have been made in the limnic basin of the Saar, where there is a complete absence of marine fauna, the associated forms being chiefly insects and chelicerates, with a few nonmarine ostracodes, branchiopods, bivalves, fishes, *Spirorbis*, and a myriapod (19). The largest most complete specimens known come also from such intermontane limnic basins, whereas specimens from paralic deposits usually occur as detached paratergal folds, axes, sternites, limbs, limb fragments, or rosette plates (8). The ever-present problem of selective diagenesis must not be overlooked, however, and it is possible that any originally calcareous shelly fauna would be dissolved during the production of humic acids in peat formation. Similarly, the tenuous condition of the *Arthropleura* cuticle may only be a reflection of these conditions, mineralized layers in the cuticle being readily dissolved under these conditions and only sclerotized tissues remaining unattacked.

From their occurrence and morphology, WATERLOT (19, 21) deduced that *Arthropleura* was amphibious. He suggested that it was predominantly a lacustrine creature, which moved slowly over the surface of marshy lake floors breathing by gill lamellae. He also envisaged that *Arthropleura* could climb out onto land and live in the undergrowth where the necessary humidity would be maintained to enable the gill plates to function. From the nature of the supposed cephalic limb, WATERLOT (20) inferred that *Arthropleura* was carnivorous and fed on small prey such as worms. Even if this limb is a gnathobasic maxilla, however, this need not imply a carnivorous owner, for such a large creature, if herbivorous, would also need powerful mouth parts to break and shred the large amount of vegetation required for sustenance. VAN DER HEIDE (10; 1956) questioned the aquatic habit, suggesting that the development of legs with pointed claws indicated that *Arthropleura* clambered among the plant debris of the boggy ground of the coal swamp.

Until the nature of the *K* plates is elucidated or spiracles are discovered, the exact way in which *Arthropleura* respired, and

hence its habit, must remain obscure. However, comparison with the form and function of modern myriapods is fruitful, thanks to the valuable body of knowledge published by MANTON (1950-65). As KOMAREK (17) has pointed out, *Arthropleura* resembles such Recent diplopods as the Polydesmida in its general habitus. According to MANTON (11, 12):

These "flat-backed" millipedes live under dead leaves and loose damp material. The lateral projection of their legs restricts their burrowing, and they cannot force their way through soil as can the juliform types. Both spines and wings will direct flattish objects away from the body, so leaving an unimpeded space in which the legs may move. The animals are thus well suited to push into crevices which give way predominantly in one plane, as does the damp layered mass of semi-decayed leaves on a woodland floor, or the bark and wood of decaying logs. The push is applied mainly by the dorsal surface or "flat back," the keels when present providing both protection for the legs and a surface of application for the force.

Such a description might well be of the habit of *Arthropleura* which may be envisaged plowing through the surface layers of the forest peat of the typical coal swamp. It is therefore improbable that *Arthropleura* could burrow, as GARSTANG (5) seems to have been the first to suggest in his verse "The trilobites and after." *Arthropleura* probably had a sluggish but powerful gait, and it would have readily fallen prey to contemporary amphibians and reptiles, doubtless *Arthropleura's* only enemies.

The gut infilling preserved in the juvenile *Arthropleura armata* previously mentioned is packed with vegetable debris. Carbonized wood tracheids with scalariform pitting are visible and fragments of epidermis are recognizable. Mr. D. BRETT, of Glasgow University Botany Department, who kindly determined these elements, states that the fragments are of lycopods. This is direct evidence that *Arthropleura* was herbivorous, and not predominantly carnivorous as WATERLOT suggested, although it does not prevent it from being an omnivore (16).

In characters such as body shape, lateral projection of the paratergal folds, lateral insertion of limbs on the body wall, and herbivorous diet, *Arthropleura* does indeed resemble the polydesmid diplopods. It is suggested that these resemblances have

been acquired by these two separate classes of myriapods as a result of parallel evolution.

The great size attained by *Arthropleura* was explained by ANDRÉE (1913) on HANDLIRSCH's theory for the giant size of Coal Measure insects. This theory suggests a correlation of such gigantism with tropical or subtropical climates, where growth is not interrupted by a pause during a cold season. MANTON (12) has stated that factors such as difficulties of molting and of tracheal respiration limit large size in arthropods, "but the power which can be put out by the legs is alone sufficient to restrict size increase in millipedes." These problems would doubtless be acute for *Arthropleura* but they can only be answered when the nature of the respiratory organs is known.

These giant arthropods were completely dependent upon the unusual environment of the Coal Measures swamp for their survival and their range in time and space coincides with that of the Euramerian floral belt, with the exception of one undescribed record from the west of the Angaran floral province (13). Thus *Arthropleura* ranges from Westphalian A to Stephanian C; PRIBYL (1960) has figured specimens from the Namurian A of Czechoslovakia but these are not certainly *Arthropleura*.

AFFINITIES AND CLASSIFICATION

In view of the conflicting opinions on the affinities of *Arthropleura*, a brief history of these views is desirable.

Prior to KLIVER's (1884) description of a specimen bearing 13 pedigerous sternites (Fig. 392), interpretations of the systematic position were understandably diverse. Thus JORDAN & MEYER (1853) originally suggested that *Arthropleura* was a decapod crustacean and later (1854) made comparisons with eurypterids and trilobites. KLIVER dissociated this arthropod from insects and arachnids and stated that it could not be a myriapod, although he presented no argument in support of this view. He regarded *Arthropleura* as a nondecapod crustacean and compared the appendages with those of the Branchiopoda. ZITTEL (1885) established the family Arthropleuridae and

pointed out that the lack of tagmosis and nature of the ventral surface differentiated the family from Isopoda and Amphipoda. Since he could not classify the Arthropleuridae with any other crustacean group, however, he suggested that it formed a connecting link between Isopoda and Amphipoda. ANDRÉE (1910) suggested that this lack of tagmosis was primitive. He inferred that since gill plates were present on at least 11 segments, but only on the fewer somites of either thorax or abdomen of Recent amphipods or isopods, respectively, *Arthropleura* is closely related to the common ancestor of the Edriophthalma (*i.e.*, Amphipoda, Tanaidacea, and Isopoda). Later (1913) he concluded that it also formed a link between the Isopoda and Schizopoda (Euphausiacea and Mysidacea). The first to have listed *Arthropleura* among the myriapods were MOYSEY & WOODWARD (in MOYSEY, 1911).

CALMAN (1913, in BROILI, 1932) concluded that *Arthropleura* is "certainly not an isopod" and criticized ANDRÉE's views. If *Arthropleura* is a crustacean, in the view of CALMAN it is "of a type hitherto unknown," but it might "even be a very generalized and primitive kind of myriapod"; CALMAN therefore referred it to Arthropoda *incertae sedis*.

The next major change in the systematic position of the group was made by WATERLOT (1934) who founded the order Arthropleurida, ranked by him as having taxonomic status equal to the Trilobita within the crustacean subclass Archaeocrustacea (later, 1949, within the Trilobitomorpha). STØRMER (1944) challenged WATERLOT's reconstruction of a biramous trilobite-like limb for *Arthropleura*. He concluded that the limb was uniramous, having "little in common with the trilobite appendage," and judged that the only trilobitan feature of *Arthropleura* was the trilobation of the tergites. STØRMER therefore only referred the genus with doubt to the Arachnomorpha.

A posthumous note on KOMAREK's views of the systematic position of *Arthropleura* was published by SHAROV (1960), who denied that *Arthropleura* is related to the Trilobita and stated, without foundation, that it is a typical representative of the

diplopod myriapod family Polydesmidae, both in leg morphology and in its paleoecology. NOVOZHILOV (1962) accordingly referred the Arthropleuridae to the Diplopoda, *Ordo incertae sedis*, in the Russian "Osnovy paleontologii."

The present writer provisionally regards the Arthropleurida as a distinct class of myriapods. Evidence for this attribution to the Myriapoda is slender, and only amounts to the lack of tagmosis of the large number of somites, presence of uniramous limbs on all known somites, and the inferred terrestrial habit. The Arthropleurida differ from other myriapod classes in the large number of their leg segments and in the presence of the rosette plate. [The coxosternopleurites of the Archipolypoda probably served to strengthen the leg bases of these large myriapods and in this respect resemble the arthropleurid rosette plate. Details of the two plates are quite different, however, and such similarity of function is to be expected in both such unusually large arthropods. If the paratergal folds of *Arthropleura* are articulated with the axis, as has been suggested, then this would suggest comparison with the "Eurysterna."]

Further details of the morphology of *Arthropleura* are needed to verify its true position within the Arthropoda, and, if the current attribution proves to be correct, to deduce its relationship to other myriapod classes. Data are needed on such critical points as: nature of the respiratory structures (tracheal or branchial), number of antennae, nature and number of mouth parts, and position of genital openings. Should *Arthropleura* prove to have gill plates and lack spiracles, then of course it could not be a myriapod, and the Arthropleurida would need to be elevated to super-class rank. *Arthropleura* would then strikingly resemble SNODGRASS' (1956, fig. 1C) hypothetical primitive walking arthropod, his "protarthropod" or even "protomandibulate." Such a gill plate would provide the only criterion for regarding *Arthropleura* as a crustacean. Although a similarly large number of trunk segments is found in the Branchiopoda, such numerous limb segments are unknown in the Crustacea, or indeed in any other arthropod group except Pycnogonida. There is thus little support at

present for GUTHÖRL's (9) view that *Arthropleura* occupied a position intermediate between the Crustacea and Myriapoda.

It is unwise to seek any fundamental phylogenetic significance in either the trilobed or onisciform habitus, since these features recur in widely separate arthropod groups and are clearly highly adaptive.

SYSTEMATIC DESCRIPTIONS

Class ARTHROPLEURIDA

Waterlot, 1934

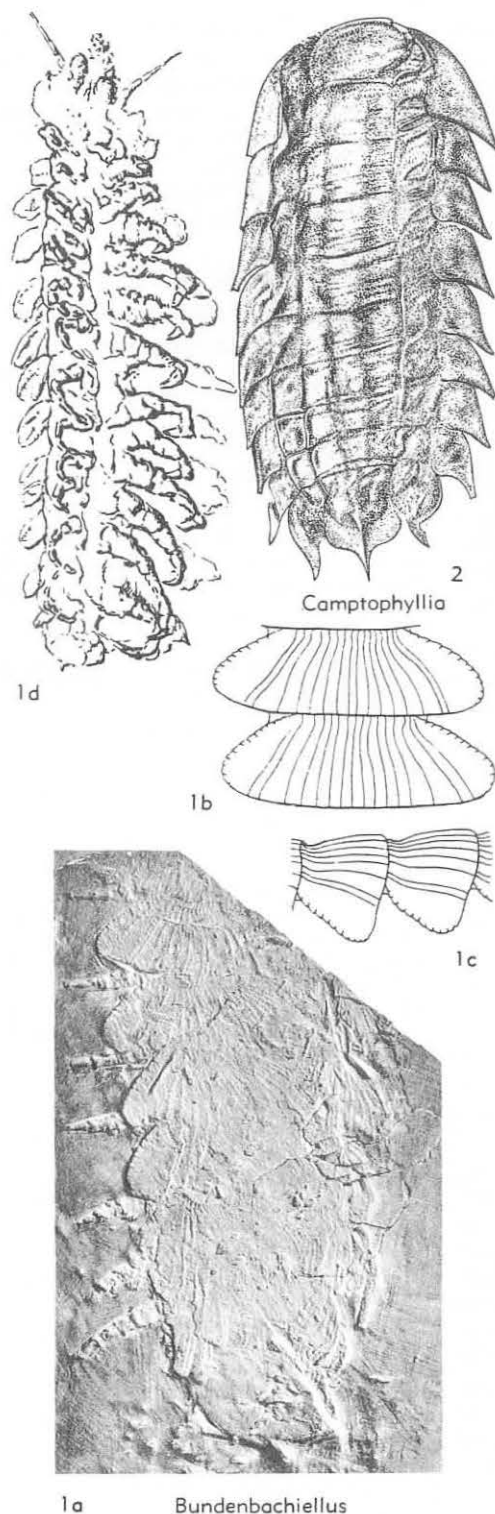
[*nom. transl.* STÖRMER, 1944 (*ex order* Arthropleurida WATERLOT, 1934)] [=Gigantopleurida GUTHÖRL, 1934]

Gigantic myriapods? with long body of more or less uniform width. Single pair of multiarticulate uniramous limbs borne by each somite, limbs characterized by numerous (8 to 10—number uncertain) of segments. Large, radially lobed subcoxal? sclerite (rosette plate) situated anterior to base of each limb. *U.Carb.*

Family ARTHROPLEURIDAE Zittel, 1885

Characters of class. *U.Carb.*

Arthropleura JORDAN & MEYER in MEYER, 1853, p. 161 [**A. armata* (= *Halongia irregularis* GEINITZ, 1855; *Macropteris punctata* GOLDENBERG, 1885; *Amynilyspes springhillensis* COPELAND, 1957); M] [= *Troxites* GOLDENBERG, 1854, p. 36 (type, *T. germari*; M); ?*Troxitis* SCUDDER, 1879 (*nom. null.*); *Arthropleura* GEINITZ, 1866 (*nom. null.*); *Arthropleuria* BOULE, 1893 (*nom. null.*); *Athroleura* GUTHÖRL, 1934 (*nom. null.*); ?*Branchipusites* GOLDENBERG, 1875, p. 23 (type, *B. anthracinus*; M); ?*Branchiopusites* GOLDENBERG, 1877 (*nom. null.*); ?*Arthropleurion* GOLDENBERG, 1877, p. 48 (type, *A. inermis*; M); ?*Athroleurion* GOLDENBERG, 1877 (*nom. neg.*); ?*Carcinochelus* GOLDENBERG, 1877, p. 34 (type, *C. anthracophilus*; M)]. Tergites dorsoventrally depressed, divided by 2 longitudinal axial furrows into 3 lobes, comprising central rectangular axis and 2 lateral subtriangular paratergal folds, all bearing prominent spines and tubercles. Probably 29 posteriorly imbricating postcephalic somites, excluding telson. Paratergal folds directed forward in anterior region of body and backward in posterior region. Head small, obovate, broader than long (poorly known). Telson unknown. Limbs inserted midway between ventral mid-line and tips of paratergal folds and separated by sternite. Each limb segment except 1st with pair of long distal spines; last segment? a claw; proximal segments with prominent ridges and grooves, anterior



face smooth, posterior tuberculate. Rosette plate separated from posterior triangular *B* plate by sulcus. *K* plate thin, variable in position. *U. Carb.*, C. Eu.-NW. Eu.-USSR (Kazakh.)-N. Am. (Can.-Ill.). —FIG. 386, 1; 387, 1. **A. armata*, Eng.; 386, 1, dorsal, $\times 2$ (Rolfe, n); 387, 1a, b, dorsal, ventral, $\times 0.1$ (16). [See also Fig. 388-392.]

TAXA DOUBTFULLY CLASSIFIABLE AS ARTHROPLEURIDA

The following two rare genera show certain similarities to *Arthropleura* but are not known in sufficient detail to be more closely compared. *Camptophyllia* is known from six specimens in Coal Measure clay-iron-stone concretions like those containing *Arthropleura* itself, whereas *Bundenbachiellus*, a possibly ancestral form, is known from two specimens from the marine Hunsrück Shale. From the intact preservation of the latter BROILI (3) concluded that *Bundenbachiellus* was an amphibious form. *Bundenbachiellus* BROILI, 1930, p. 219 [*nom. subst. pro Megadactylus* BROILI, 1929, p. 141 (*non* FITZINGER, 1843, *nec* HITCHCOCK, 1865)] [**Megadactylus giganteus* BROILI, 1929; M]. Body elongate, with at least 8 somites; tergites broad, with longitudinal, posteriorly diverging, spined ridges; anterolateral edges of paratergal folds notched and setose; ?telson subcircular. At least 7 pairs of uniramous limbs emerging between somites, 1 pair per somite; limbs with at least 6 segments distally, last a claw. [Compared with Myriapoda, Isopoda and Syncarida by BROILI (2,3) who concluded that if it was not a myriapod, then it represented an undescribed group of Crustacea. Prior to this, HENNIG (1922, p. 144-145) had suggested a comparison with *Arthropleura*. Another specimen, described as *B? minor* by BROILI (3), is even more myriapod-like in showing the head with a single pair of antennae (although a 2nd pair might also be present according to BROILI), 12 body somites with large paratergal expansions, 1st 2 body somites smaller, 3rd and 4th larger than other somites; single pair of uniramous limbs per somite, 6- or 7-segmented, last digit clawlike. ?Telson semicircular.] *L. Dev. (Siegen.)*, Eu. (Ger.). —FIG. 393, 1a-c. **B. giganteus* (BROILI), Hunsrück Sh.; 1a, holotype, dors., $\times 0.5$; 1b, c, 2 tergites, dorsal, lat., spinules on longitudinal ridges not shown (2). —FIG. 393, 1d. *B? minor* BROILI, Hunsrück Sh.; holotype, ventral, $\times 2.0$ (3).

FIG. 393. Doubtful taxa, Arthropleurida (p. R618-R619).

Camptophyllia GILL, 1924, p. 466 [**C. eltringhami*; OD]. Body elongate, approximately twice as long as greatest breadth; slightly depressed, onisciform; of 10 posteriorly imbricating somites (telson excluded), bearing low, elongate granules; somites divided by 2 longitudinal axial furrows into 3 lobes, each somite with median axis and 2 lateral, posteriorly directed paratergal folds; 1st somite semicircular, paratergal folds extending posteriorly to cover 2nd somite laterally; axis one-third width of body at center, narrowing anteriorly and more so posteriorly; with 1 median and 2 lateral, longitudinal, low ridges. Head unknown (probably concealed beneath 1st segment). Telson oval, posteriorly acuminate, with prominent dorsal keel or tubercle. [Originally described as *Arthropoda incertae sedis* and compared with *Isopoda*; PEACH regarded it as an "aberrant millipede." Referred conditionally to *Arthropleurida* by BROOKS (1962).] *U. Carb. (Westphal. B, similis-pulchra Zone)*, Eng. (Durham-S.Staffs.).—FIG. 393,2. **C. eltringhami*, Durham; holotype, dorsal, post. border of 10th segment not shown, $\times 2$ (6).

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